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WINTER MOVEMENTS AND SPRING MIGRATION OF AMERICAN WOODCOCK ALONG THE ATLANTIC COAST

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Abstract.—Radio transmitters were attached to American Woodcock (*Scolopax minor*) at three Atlantic coastal sites to monitor winter movements and spring departure dates from Georgia (1982–1984, 1989–1991), South Carolina (1988–1989), and Virginia (1991–1992). There was no evidence of temperature, sex, or age-dependent migration dates. Migration was coincident with the full moon in February and the passage of weather fronts close to this time. *Received 13 Sept. 1993, accepted 1 Feb. 1994.*

Little is known about the spring migration of American Woodcock (*Scolopax minor*) other than that they generally leave wintering grounds beginning from late January to late February (Glasgow 1958, Pace and Wood 1979, Tappe et al. 1989, Olinde and Prickett 1991, Roberts 1993) and arrive on northern breeding grounds in late March and April (Sheldon 1971, Sepik et al. 1993). Initiation of spring migration may depend on temperature, with earlier departures during warmer winters and later departures during colder winters (Glasgow 1958, Martin et al. 1970, Roberts 1993), and may span several weeks at any one location (Roberts 1993). Moon phase, passage of weather fronts, day length, and reproductive state also may trigger the initiation of spring migration (Coon et al. 1976, Olinde and Prickett 1991). Sex-specific migration chronology has been alluded to, with males migrating earlier than females (Glasgow 1958, Martin et al. 1970, Owen 1977); however, both sexes appear to arrive at the breeding grounds simultaneously (Dwyer et al. 1988, Sepik et al. 1993).

All knowledge of woodcock spring migration is based on banding studies and anecdotal evidence. While this information is valuable, data obtained using radio telemetry is more reliable. During six winters between 1982 and 1991, we attached radio transmitters to woodcock at three wintering sites along the Atlantic coastal plain. We addressed three questions: (1) Does spring migration commence earlier during colder winters than during warmer winters?, (2) Is spring migration more variable during colder winters than during warmer winters?, and (3) Is there a difference between the spring departure dates by sex or age?

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STUDY AREA AND METHODS

We used three study sites along the lower Atlantic coastal plain. The first included the southern shore of the Altamaha River near Everett, Georgia, where the predominant habitat is timberland managed primarily for pulpwood. Pine (*Pinus* spp.) plantations were clear-cut, followed by intensive post-cutting management. The second study area was within the Francis Marion National Forest (FMNF) near McClellanville, South Carolina. This forest (100,000 ha) was 98% forested with about 75% in managed pines and the remaining 25% in bottomland hardwoods. The forest was managed intensively for timber production, using mostly clear-cutting, and enhancement of Red-cockaded Woodpecker (*Picoides borealis*) habitat. The third study area was the Eastern Shore of Virginia National Wildlife Refuge (ESVNWR) on the southern tip of the Delmarva Peninsula near Cape Charles, Virginia. It was agricultural fields scattered among older woodlots of mixed pines-hardwoods. Little forest management was evident in the area.

All three study areas were characterized by relatively mild winter weather. The mean number of days with the daily minimum temperature ≤0°C from December through February recorded at the weather stations closest to the study areas were: Norfolk, Virginia, 45 days; Pinopolis Dam, South Carolina, 37 days; Waycross, Georgia, 30 days (1951–1975; NOAA 1978). Soil temperatures at 10 cm depth were rarely <0°C (NOAA 1982–1992); any freezing of the soil at the surface was of short duration.

Study dates by site were (1) Georgia: 29 December 1982–3 March 1983; 14 December 1983–1 March 1984; 16 December 1989–15 February 1990; 28 December 1990–15 March 1991; (2) South Carolina: 14 December 1988–18 February 1989; and (3) Virginia: 9 December 1991–6 March 1992. Data were collected in Georgia during two studies: one during 1982–1984 (G. Haas, U.S. Fish Wildlife Service [USFWS], unpubl. data) and one during 1989–1991. The South Carolina study site was abandoned because of damage by Hurricane Hugo, and the Virginia study site was used only one winter. Due to the confounding of years and locations, any differences cannot be attributed only to year or location. Hereafter we refer to this combined effect as ''year (location).''

Woodcock were captured using ground traps (Liscinsky and Bailey 1955), mist nets (Sheldon 1971), and nightlighting (Riefenberger and Kletzly 1967). They were banded with USFWS leg bands, weighed, aged, and sexed (Martin 1964, Mendall and Aldous 1943). A radio transmitter was attached to each bird dorsally between its wings, using a single multistrand wire loop harness and livestock tag cement (McAuley et al. 1993). Transmitters weighed 3.5–5.0 g, were attached to individual birds, and did not exceed 3% of body mass. This harness design does not inhibit normal behavior (McAuley et al. 1993). During every year, we tested 5% of the radios to determine if they met our specifications of ≥60 day life. In all years, all tested radios met this criterion.

During 1988–1992, we tried to capture 50 woodcock per year. Capture efforts continued until the sample size was obtained or until 31 January. Marked birds were tracked daily except during 14 February–15 March 1991 when locations were checked weekly, using vehicle-mounted four- or seven-element Yagi antennas. Once located, the status (alive, dead) of each bird was determined, using signal modulation. Woodcock classified as 'censored' included those birds whose fates were unknown, excluding birds which had died. If status could not be determined using signal modulation, the location of the bird was determined by approaching on foot for a visual sighting. The location of each bird was estimated to the nearest 50 × 50 m block. If a bird did not move within 48 h, we attempted to flush or recover it. We searched for lost birds from aircraft (Gilmer et al. 1981) within a 50-km radius of the center of the study area. If they could not be located from the air, we searched for lost birds from vehicles. Only censored birds are included in the present analyses.

A few woodcock were still present on the study areas when tracking was terminated. These birds were not included in the analyses because they may have been residents. We defined the migration date for each bird as the last day that the bird was located alive (censoring date). No birds censored before 16 January were included in these analyses, because birds disappearing before then probably were not permanently migrating (Glasgow 1958, Roberts 1993). We tested the effect of temperature on migration date by means of linear regression. We regressed the median censoring date by year against the mean daily minimum temperature spanning, either 15 December–5 February or 15 January–5 February, or against the average of the daily minimum temperature for the two weeks preceding each bird's censoring date.

Because spring migration may span several weeks at a given location (Roberts 1993), variation in spring migration may be weather-dependent. Weather could conceivably influence spring migration through the negative effect of cold temperatures on food availability. If food availability is more variable during colder years, then we hypothesize that variation in spring migration would be less in colder years because woodcock should not risk migrating when food availability to the north is questionable. That is, spring migration would be delayed until food availability is assured, and then all migrants would leave over a short time period. To test this hypothesis, we used linear regression to relate the standard deviation of censoring dates against the three temperature metrics mentioned above.

Use of censoring dates as an index of migration is not without fault as censoring can result from undetected death, temporary emigration, or radio failure. This could bias our analyses by suggesting that migration occurred earlier or in a different pattern than it did. This problem is important when censoring, unrelated to migration, varied among years (locations).

As a measure of winter severity, we used the mean daily minimum temperature (°C). We began the first mean at mid-December because, in most years, woodcock were present then at all sites (Pursglove 1975, Stamps and Doerr 1976), making this measurement representative of temperatures during the entire winter. Starting the mean at mid-January was much closer to when most woodcock migrated and might represent a late winter fine tuning of migration date. The final temperature measurement of the three is the most closely tied to the temperatures when birds actually were censored of the three measurements. We believe that daily minimum temperature is a relevant index to winter severity because earthworms (Lumbricidae), the primary food of woodcock (Cade 1985), are less available to woodcock during freezing temperatures (Reynolds et al. 1977, Stribling and Doerr 1985a).

Because year and location were confounded, we conducted two separate analyses. The first analysis used data from all six years, and the second, to avoid potential interaction among locations (latitude) and migration date, used only data collected in Georgia (four years).

We used a three-way ANOVA to test for the effects of sex, age, and year (location) on migration date. All interactions of the factors were included in the analysis. Analyses were conducted with all data and with Georgia data alone.

RESULTS

To address the use of censored birds as a measure of migration date, we evaluated several alternative explanations of censoring other than migration (see above). Undetected mortalities could have resulted from hunter kills not immediately reported. However, the only hunter kill reported to the USFWS Bird Banding Laboratory was a woodcock killed in the winter after it was marked, and only one hunter was encountered (several times) during the study. Temporary movements could be a problem if those birds moved away from the study area but remained on the wintering grounds before beginning spring migration. During three winters (1988–1989, 1990–1991, 1991–1992), we documented five of 202 marked birds (2%) which moved from the study area, were not detected for ≥5 days during searches, and subsequently returned.

We did document marked birds permanently leaving the study area before the end of observations each year. These few woodcock remained near the study area for at least several days before being censored. One woodcock at Georgia 1982–1983 moved 14.5 km to the northwest along the Altamaha River. This bird remained at this location for two days and then was censored on 25 February 1983. One woodcock at Georgia in 1983–1984 moved 33.8 km to the northwest along the Altamaha River where it remained for one day and was censored on 8 February 1984. Three woodcock at South Carolina 1988–1989 began wandering northward from late December to mid-January. These birds moved between 2.9–3.6 km north across the Santee River before being censored in mid-February 1989. At Georgia 1990–1991, nine woodcock moved west around 29 January 1991 when the study area was flooded by the Altamaha River. These birds moved between 3.5–7.5 km before being censored: two in late January 1991 and seven in mid-February 1991. In Virginia in 1991–1992, one woodcock moved north 11 km and remained at that location for three days before being censored on 21 February 1992. Except for woodcock which were displaced by floodwaters in Georgia 1990–1991, the general pattern for migrating birds was a north to northwest movement ≥2 km. These birds remained at their new location for 1–3 days and then were censored. In no year or location did a woodcock move ≥2 km to the north or northwest and then return to the study area.

Median dates of censoring among years ranged from 1–22 February. The mean temperature for the entire winter ranged from 0.20–7.02°C, for the latter part of winter it ranged from −1.97–7.32°C, and for the average of the two weeks preceding censoring it ranged from −0.13–7.77°C. The coldest winter occurred in Virginia 1991–1992, while the warmest winter occurred in Georgia 1989–1990. All temperature measurements changed in the same direction between years, i.e., they all went up or down in unison, but due to temperature fluctuations within years, the measurements did not reflect one another in magnitude within years. For example, in 1982, the whole winter, late winter, and two-week mean temperatures reflected each other closely (3.30 vs 3.38 vs 3.39, respectively), whereas in 1983, the means did not (3.60 vs 5.15 vs 4.98, respectively).

Sample sizes by year and location were low in Georgia 1982–1983 and in South Carolina 1988–1989 but were adequate in all other years (lo-

TABLE 1
SAMPLE SIZES OF AMERICAN WOODCOCK WINTERING ALONG THE ATLANTIC COAST USED IN SPRING MIGRATION ANALYSES BY AGE, SEX AND YEAR (LOCATION)[a]

Year	Location	Young male	Young female	Adult male	Adult female
1982–1983	Georgia	8	3	2	1
1983–1984	Georgia	19	11	7	7
1988–1989	South Carolina	6	3	0	2
1989–1990	Georgia	21	8	5	4
1990–1991	Georgia	21	11	3	15
1991–1992	Virginia	21	17	2	5

[a] Because not all locations were represented every year, year (location) represents the confounding effects of year and location.

cations) (Table 1). No significant relationship ($P > 0.10$) was noted between median censoring date and any temperature measurement (Table 2, Fig. 1). All slopes were negative which was the expected direction. The direction of the slope was determined by Virginia 1991–1992 data when migration occurred late and temperatures were low. When only data from Georgia were analyzed, no significant relationships ($P > 0.10$) were

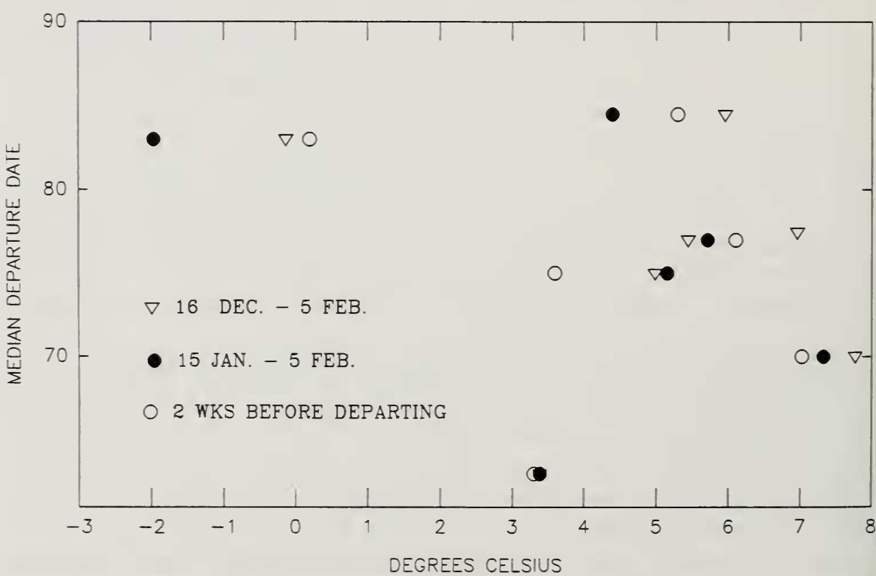

FIG. 1. Relationships between three winter temperature measurements and spring migration dates of American Woodcock wintering in coastal sites in Georgia, South Carolina, and Virginia between 1982 and 1991.

TABLE 2

RELATIONSHIP BETWEEN THREE WINTER TEMPERATURE MEASUREMENTS AND SPRING MIGRATION DATES OF AMERICAN WOODCOCK WINTERING ALONG THE ATLANTIC COAST FOR ALL SITES AND YEARS AND FOR GEORGIA

Response variable	Predictive equation	t[a]	P
All sites and years			
MCD[b]	= 78.4 − 0.712 ($\bar{x}$ MDT[c] 15 Dec.–5 Feb.)	−0.44	0.68
MCD	= 79.3 − 0.968 ($\bar{x}$ MDT 15 Jan.–5 Feb.)	−0.83	0.45
MCD	= 78.5 − 0.670 ($\bar{x}$ MDT for 2 wks. before censoring date)	−0.46	0.67
SD MCD[d]	= 13.4 − 0.627 ($\bar{x}$ MDT 15 Dec.–5 Feb.)	−0.95	0.40
SD MCD	= 12.1 − 0.339 ($\bar{x}$ MDT 15 Jan.–5 Feb.)	−0.64	0.56
SD MCD	= 12.7 − 0.426 ($\bar{x}$ MDT for 2 wks. before censoring date)	−0.68	0.54
Georgia			
MCD	= 66.9 + 1.304 ($\bar{x}$ MDT 15 Dec.–5 Feb.)	0.36	0.75
MCD	= 71.6 + 0.298 ($\bar{x}$ MDT 15 Jan.–5 Feb.)	0.08	0.95
MCD	= 63.0 + 1.833 ($\bar{x}$ MDT for 2 wks. before censoring date)	0.57	0.63
SD MCD	= 20.7 − 1.848 ($\bar{x}$ MDT 15 Dec.–5 Feb.)	−2.14	0.17
SD MCD	= 23.4 − 2.278 ($\bar{x}$ MDT 15 Jan.–5 Feb.)	−46.54	<0.001
SD MCD	= 22.4 − 1.906 ($\bar{x}$ MDT for 2 wks. before censoring date)	−3.26	0.08

[a] t is for test of significance of slope $\neq 0$.
[b] MCD = mean censoring data.
[c] MDT = minimum daily temperature.
[d] SD MCD = standard deviation of MCD.

evident (Table 2). Slopes were positive for the Georgia analyses although opposite of the expected direction. These slopes were indicative of the results obtained when the Virginia data were excluded.

Spring migration dates were variable across years, with Georgia 1982–1983 having the highest variability (SD = 15.76) and Georgia 1989–1990 had the lowest variability (SD = 6.72). No significant relationship ($P > 0.10$) was found between the standard deviation of censoring dates and any temperature measurement (Table 2). All slopes were negative which was opposite of the expected direction. Examining only data from Georgia revealed that no relationships ($P > 0.10$) were evident for the mean minimum temperature for the entire winter or the running mean temperature for two weeks preceding censoring, but a significant relationship ($P < 0.001$) existed for the minimum temperature for the late winter (Table 2). However, the slope was negative, opposite of the expected direction.

We found no effect of sex or age on spring migration dates (Table 3),

TABLE 3

RELATIONSHIP AMONG SEX, AGE, YEAR (LOCATION)[a] AND SPRING MIGRATION OF AMERICAN WOODCOCK

Source	df	MSE[b]	F	Pr > F
All sites and years				
Sex	1	0.664	0.00	0.95
Age	1	176.8	0.89	0.35
Year (location)	5	478.4	2.40	0.04
Sex*age	1	0.046	0.00	0.99
Age*year (location)	5	252.4	1.27	0.28
Sex*year (location)	5	128.8	0.65	0.66
Sex*age*year (location)	4	145.9	0.73	0.57
Error	179			
Georgia				
Sex	1	3.997	0.02	0.89
Age	1	74.19	0.37	0.54
Year	3	536.7	2.68	0.05
Sex*age	1	44.16	0.22	0.64
Age*year	3	348.3	1.74	0.16
Sex*year	3	154.7	0.77	0.51
Sex*age*year	3	116.5	0.58	0.63
Error	130			

[a] Because not all locations were represented every year, year (location) represents the confounded effects of year and location.
[b] MSE = Mean squared error.

although adults were poorly represented in all years (Table 1). An effect of year (location) was found with woodcock migrating significantly later from Virginia 1991–1992 and Georgia 1990–1991 than for the remaining years (locations) (SNK, $P = 0.05$). Using Georgia data, there was no effect of sex or age on spring migration dates (Table 3). Year was important, with woodcock leaving later during 1990–1991 than during other years (SNK, $P = 0.05$).

During two years (South Carolina 1988–1989, Georgia 1989–1990), there was a concentration of woodcock censored over a one-week period (Fig. 2). Coon et al. (1976) commented that fall migrating female woodcock departed shortly before a full moon. In both years, of those woodcock still present one week before the full moon in February, 90% in both South Carolina 1988–1989 and Georgia 1989–1990 were censored before the full moon. During the remaining four years, between 64–100% of the birds alive until one week before the full moon in February were censored within two weeks.

Coon et al. (1976) noted that fall migrating female woodcock generally

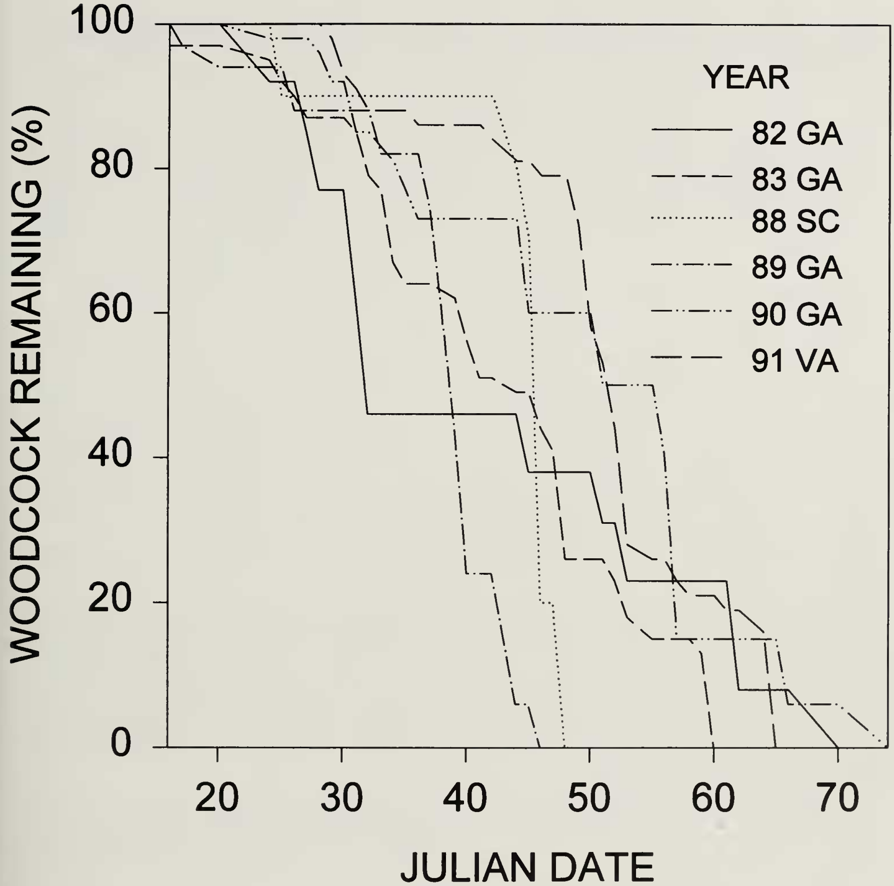

FIG. 2. Censoring dates for American Woodcock during spring migration from coastal sites in Georgia, South Carolina, and Virginia between 1982 and 1991.

departed when cold fronts approached and winds blew from the northwest. We, too, found that the passage of fronts was coincident with ≥ five woodcock departing in different years. Excluding Georgia 1982–1983, when no more than two birds per day were censored, concentrations of woodcock were censored <24 h after a front passed and the wind blew from the south or southwest (NOAA 1982–1992). Further, in the three years noted above, when a large percentage of the remaining woodcock were censored over a short period, during the two weeks around the full moon, northerly winds blew for about 65% of the time while winds from the south or southwest occurred only for about 20% of the time (NOAA

1982–1992). The birds moved when the wind blew from a southerly direction.

DISCUSSION

The reasons that woodcock initiate spring migration are probably many but likely include the advantages of arriving early at the breeding grounds (Sheldon 1971, Sepik et al. 1993), access to increased food resources (Gauthreaux 1982), and increased survivorship (Greenberg 1980). The mechanisms triggering migration in woodcock include photoperiod, weather, and possibly reproductive state (Coon et al. 1976, Olinde and Prickett 1991, Roberts 1993). Based on our analyses, mean minimum temperatures during the winter were not related to spring departure. Although we found no relationship between winter temperatures and spring migration, we do advise some caution with this interpretation because of the small sample size. We calculated the power to detect a correlation with six or four years of data and a true correlation of 0.1; the observed correlations were <10%. Estimated powers were 13 and 12%, respectively.

The apparent absence of temperature dependent migration and the coincidence between censoring and the moon phase suggested that migration is fairly constant among years. Such consistency agrees with the observation that on the Maine breeding grounds, woodcock arrive each year on about the same date (Dwyer et al. 1988, Sepik et al. 1993, but see Mendall and Aldous 1943).

Variability in the migration dates within a year was great and was related to late winter temperatures in Georgia. Apparently warmer temperatures concentrate the departure of migrating woodcock but not necessarily towards earlier dates. Again we are somewhat hesitant in drawing this conclusion because only one of six regressions demonstrated a significant relationship, although all slopes were negative.

The notion that spring migration is sex- or age-specific was not supported. We believe that the apparent disparate migration of woodcock by sex or age results from misinterpreting banding data as has been suggested previously (Stribling and Doerr 1985b, Diefenbach et al. 1990, Sepik et al. 1993). Female woodcock tend not to frequent nocturnal roosting fields at the same rate or possibly in the same location as males (Owen and Morgan 1975, Horton and Causey 1979, Stribling and Doerr 1985a, Sepik et al. 1993). Because most capture methods rely on capturing woodcock on roosting fields, the potential for a biased sample ensues.

We did find an association between spring departure and both moon phase and the passage of weather fronts. The association between spring departure and the full moon is intriguing because of the reluctance by wintering woodcock to enter or remain in nocturnal fields around the time of the full moon (Glasgow 1958; USFWS, unpubl. data). Possibly the concern over nocturnal predators (Dunford and Owen 1973) is superseded by the aid of moonlight in navigating. The association between migration and the passage of weather fronts has been noted in other species (Gauthreaux 1982). The movement of weather fronts and the switch in the wind direction provided beneficial conditions which triggered or ''released'' woodcock to migrate (Coon et al. 1976).

Sheldon (1971) and Owen (1977) hypothesized that woodcock usually undergo partial migrations in response to winter temperatures. Accordingly, woodcock remain as far north as the temperatures allow at the beginning of the winter and move southward in response to declining temperatures. Whether woodcock return to their previous locations after temperatures ameliorate is not clear (Owen 1977). Exceptions to these partial migrations in response to cold temperatures do occur, as Sheldon (1971) and Mendall and Aldous (1943) noted that large numbers of woodcock sometimes die during cold weather rather than migrate southward. Our data spanned six years between 1982 and 1992, and within each winter, ≤ five woodcock per day were censored at any time between mid-December and the first week in February (unpubl. data). This pattern held true even in the last week of December 1989 when a severe cold front moved into Georgia, reducing the daily temperature to below freezing for one week and was accompanied by a rare snowfall. The pattern of censoring within the years we examined was not indicative of partial migration, i.e., once woodcock arrived at their coastal wintering site, they remained there until spring migration.

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